Dualities in population genetics: a fresh look with new dualities.

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Abstract

We apply our general method of duality, introduced in [6], to models of population dynamics. The classical dualities between forward and ancestral processes can be viewed as a change of representation in the classical creation and annihilation operators, both for diffusions dual to coalescents of Kingman's type, as well as for models with finite population size.

Next, using $SU(1,1)$ raising and lowering operators, we find new dualities between the Wright-Fisher diffusion with d types and the Moran model, both in presence and absence of mutations. These new dualities relates two forward evolutions. From our general scheme we also identify self-duality of the Moran model.

1 Introduction

In the works [6, 7] duality between two stochastic processes, in the context of interacting particle systems and non-equilibrium statistical mechanics, has been related to a change of representation of an underlying algebra. More precisely, if the generator of a Markov process is built from lowering and raising operators (in physics language creation and annihilation operators) associated to a Lie algebra, then different representations of these operators give rise to processes related to each other by duality. The intertwiner between the different representations is exactly the duality function. Furthermore, self-dualities can be found using symmetries related to the underlying Lie algebra (see also [15]).

The fact that generators can be built from raising and lowering operators is a quite natural assumption. E.g., in interacting particle systems dynamics consists of removing particles at certain places and putting them at other places. If the rates of these transitions are appropriately chosen, then the operators of which the effect is to remove or to add a particle (with appropriate coefficients) form a Lie algebra. For diffusion processes the generator is built from a combination of multiplication operators and (partial) derivatives. For specific choices, these correspond to differential operator representations of a Lie algebra. If this Lie algebra then also possesses a discrete representation, then this can lead to a duality between a diffusion process and a process of jump type, such as the well-known duality between the Wright-Fisher diffusion and the Kingman's coalescent.

It is the aim of this paper to show that this scheme of finding dual processes via a change of representation can be applied in the context of mathematical population genetics. First, we give a fresh look at the classical dualities between processes of Wright-Fisher type and their dual coalescents. These dualities correspond to a change of representation in the creation and annihilation operators generating the Heisenberg algebra. For population models in the diffusion limit (infinite population size limit) the duality comes from the standard Heisenberg generators $x, d/dx$ and another discrete representation, known as the Doi-Peliti representation. The intertwiner is in this case simply the function $D(x,n) = x^n$. In the case of finite population size, dualities arise from going from a finite-dimensional representation (finite dimensional creation and annihilation operators satisfying the canonical commutation relations) towards the Doi-Peliti representation. The intertwiner is exactly the hypergeometric polynomial found e.g. in [10], [9], and gives duality between the Moran model with finite population size and the Kingman's coalescent.

Next we use the $SU(1,1)$ algebra to find previously unrevealed dualities between the discrete Moran model with (or without) mutation and the Wright Fisher diffusion with (or without) mutation, as well as self-duality of the discrete Moran model with mutation.

These are in fact applications of the previously found dualities between the Brownian energy process and the symmetric inclusion process, as well as the self-duality of the symmetric inclusion process, which we have studied in another context in [6], [7], [8]. Put into the context of population dynamics, these dualities give new results for the multi-type Moran model with or without mutation, as well as the multi-type Wright Fisher model with or without mutations.

The rest of our paper is organized as follows. In section 2 we give the general setting and view on duality. Though many elements of this formalism are already present in previous papers, we find it useful to put these together here in a unifying, more transparent and widely applicable framework. In section 3 we discuss dualities in the context of the Heisenberg algebra. This leads to dualities between diffusions and discrete processes, as well as between different diffusion processes, and finally between different discrete processes. In section 4 we show how this gives the dualities between forward (in time) population processes and their ancestral dual coalescents. In section 5 we apply the $SU(1,1)$ algebra techniques, developed previously in [7] in the context of population dynamics, finding new dualities, this time between two forward (in time) processes: duality between the Wright-Fisher diffusion and the Moran model, and duality of the Moran model with itself. We give three concrete computations using these new dualities as an illustration.

2 Abstract Setting

2.1 Functions and operators.

Let $\Omega, \widehat{\Omega}$ be metric spaces. $\mathscr{C}(\Omega), \mathscr{C}(\widehat{\Omega}), \mathscr{C}(\Omega \times \widehat{\Omega})$ denote the sets of bounded continuous real-valued functions on $\Omega, \widehat{\Omega}, \Omega \times \widehat{\Omega}$. In what follows, this choice of function space is not stringent, and can be replaced if necessary by other function spaces such as L^p spaces or Sobolev spaces.
For a function $\psi : \Omega \times \widehat{\Omega} \to \mathbb{R}$ and linear operators $K : \mathcal{D}(K) \subset \mathscr{C}(\Omega) \to \mathscr{C}(\Omega)$, $\widehat{K} : \mathcal{D}(\widehat{K}) \subset \mathscr{C}(\widehat{\Omega}) \to \mathbb{R}$ we define the left action of K on ψ and the right action of $\widehat{K}$ on ψ via

$$(K_l \psi)(x,y) = (K\psi(\cdot, y))\,(x)\ , \qquad (\widehat{K}_r \psi)(x,y) = (\widehat{K}\psi(x,\cdot))(y)\ , \qquad (1)$$

where we assume that ψ is such that these expressions are well-defined, i.e. $\psi(\cdot, y) \in \mathcal{D}(K), \psi(x, \cdot) \in \mathcal{D}(\widehat{K})$.
An important special case to keep in mind is $\Omega = \{1, \dots, n\}$ and $\widehat{\Omega} = \{1, \dots, m\}$ finite sets, in which case we identify functions with column vectors. In that case, an operator K (resp. $\widehat{K}$) on functions on Ω (resp. $\widehat{\Omega}$) coincides with a $n \times n$ (resp. $m \times m$) matrix. Denoting by $\mathbb{K}$ (resp. $\widehat{\mathbb{K}}$)

such matrices, one has

$$K_l\psi(x,y) = \sum_{z\in\Omega} \mathbb{K}(x,z)\psi(z,y) = (\mathbb{K}\psi)(x,y)\ , \tag{2}$$

$$\widehat{K}_r\psi(x,y) = \sum_{u\in\widehat{\Omega}} \widehat{\mathbb{K}}(y,u)\psi(x,u) = (\psi\widehat{\mathbb{K}}^T)(x,y)\ . \tag{3}$$

Namely, left action of K corresponds to left matrix multiplication and right action of $\widehat{K}$ corresponds to right multiplication with the transposed matrix. The same picture arises when $\Omega, \widehat{\Omega}$ are countable sets.
For two operators K_1, K_2 working on the same domain we denote, as usual, K_1K_2 their product or composition, i.e.

$$(K_1K_2f)(x) = (K_1(K_2f))\,(x)\ .$$

We further abbreviate $\mathscr{B}(\Omega)$ for algebras of linear operators working on a common domain of functions in $\mathscr{C}(\Omega)$. These algebras are often representation of an abstract algebra $\mathscr{H}$ (such as e.g. the Heisenberg algebra). For a general algebra $\mathscr{H}$, we define the dual algebra $\mathscr{H}^*$ as the algebra with the same elements as in $\mathscr{H}$ but with product "$*$" defined by $a * b = b \cdot a$, where $\cdot$ is the product in $\mathscr{H}$. A typical example in the finite dimensional setting is the algebra of $n \times n$ matrices, where the map $A \to A^T$ maps the algebra into the dual algebra ($(AB)^T = B^TA^T$).

Definition 2.1. *For a function $\psi : \Omega \times \widehat{\Omega} \to \mathbb{R}$ we say that ψ is left exhaustive if the relation $K_l\psi = 0$ implies $K = 0$, and correspondingly we call ψ right exhaustive if the relation $\widehat{K}_r\psi = 0$ implies $\widehat{K} = 0$. Notice that in the context of finite sets $\Omega, \widehat{\Omega}$ this just means that the matrix associated to ψ is invertible.*

2.2 Duality

Definition 2.2. *Let $K \in \mathscr{B}(\Omega)$, $\widehat{K} \in \mathscr{B}(\widehat{\Omega})$ and $D : \Omega \times \widehat{\Omega} \to \mathbb{R}$. Then we say that K and $\widehat{K}$ are dual to each other with duality function D if*

$$K_lD = \widehat{K}_rD\ . \tag{4}$$

We denote this property by $K \to^D \widehat{K}$.

In the following we collect elementary but important properties of the relation $\to^D$. The proof of these properties is elementary and left to the reader.

Theorem 2.1. *Let $K_1, K_2 \in \mathscr{B}(\Omega)$, $\widehat{K}_1, \widehat{K}_2 \in \mathscr{B}(\widehat{\Omega})$. Suppose that $K_1 \to^D \widehat{K}_1$, $K_2 \to^D \widehat{K}_2$, and further $c_1, c_2 \in \mathbb{R}$ then we have*

1. *$\widehat{K}_1 \to^{\tilde{D}} K_1$, with $\tilde{D}(x,y) = D(y,x)$.*

2. $c_1K_1 + c_2K_2 \to^D c_1\widehat{K}_1 + c_2\widehat{K}_2$.

3. $K_1K_2 \to^D \widehat{K}_2\widehat{K}_1$, *in particular* $K_1^n \to^D \widehat{K}_1^n$, $n \in \mathbb{N}$.

4. $[K_1, K_2] \to^D [\widehat{K}_2, \widehat{K}_1] = -[\widehat{K}_1, \widehat{K}_2]$, *i.e., commutators of dual operators have opposite sign.*

5. *If* $S \in \mathscr{B}(\Omega)$ *commutes with* K_1, *then* $K_1 \to^{S_l D} \widehat{K}_1$, *and if* $\widehat{S} \in \mathscr{B}(\widehat{\Omega})$ *commutes with* $\widehat{K}_1$, *then* $K_1 \to^{\widehat{S}_r D} \widehat{K}_1$.

6. *If for a collection* $\{K_i, i \in I\} \subset \mathscr{B}(\Omega)$, *and* $\{\widehat{K}_i : i \in I\} \subset \mathscr{B}(\widehat{\Omega})$ *we have* $K_i \to^D \widehat{K}_i$ *then every element of the algebra generated by* $\{K_i, i \in I\}$ *is dual to an element of the algebra generated by* $\{\widehat{K}_i : i \in I\}$. *More precisely:*

$$K_{i_1}^{n_1} \dots K_{i_k}^{n_k} \to^D \widehat{K}_{i_k}^{n_k} \dots \widehat{K}_{i_1}^{n_1} \tag{5}$$

for all $n_1, \dots, n_k \in \mathbb{N}$, *and for constants* $\{c_i : i \in I\}$

$$\sum_{i\in I} c_i K_i \to^D \sum_{i \in I} c_i \widehat{K}_i \; .$$

7. *Suppose (only in this item) that* $K_1 \in \mathscr{B}(\Omega_1)$, $\widehat{K}_1 \in \mathscr{B}(\widehat{\Omega}_1)$, $K_2 \in \mathscr{B}(\Omega_2)$, $\widehat{K}_2 \in \mathscr{B}(\widehat{\Omega}_2)$. *If* $K_1 \to^{D_1} \widehat{K}_1$ *and* $K_2 \to^{D_2} \widehat{K}_2$, *then* $K_1 \otimes K_2 \to^{D_1 \otimes D_2} \widehat{K}_1 \otimes \widehat{K}_2$, *where* $D_1 \otimes D_2(x_1, x_2; y_1, y_2) = D_1(x_1, y_1)D_2(x_2, y_2)$.

8. *If* K *and* $\widehat{K}$ *generate semigroups* $S_t = e^{tK}$ *and* $\widehat{S}_t = e^{t\widehat{K}}$ *then* $K \to^D \widehat{K}$ *implies* $S_t \to^D \widehat{S}_t$. *If moreover these semigroups correspond to Markov processes* $\{X_t, t \geq 0\}, \{\widehat{X}_t, t \geq 0\}$ *on* $\Omega, \widehat{\Omega}$, *the relation* $S_t \to^D \widehat{S}_t$ *reads in terms of these processes:*

$$\mathbb{E}_x D(X_t, \widehat{x}) = \mathbb{E}_{\widehat{x}} D(x, \widehat{X}_t) \; , \tag{6}$$

for all $x \in \Omega, \widehat{x} \in \hat{\Omega}$ *and* $t > 0$. *On the left-hand side of the above equation we have expectation with respect to the the law of the* $\{X_t\}_{t\geq 0}$ *process started at* x, *while on the right-hand side we have expectation with respect to the law of the* $\{\widehat{X}_t\}_{t\geq 0}$ *process initialized at* y.

Remark 2.1. *Item 6 of theorem 2.1 is useful in particular if the collection* $\{K_i, i \in I\} \subset \mathscr{B}(\Omega)$ *is a generating set for the algebra. Indeed, then every element of the algebra has a dual by (5), and it suffices to know dual operators for the generating set to infer dual operator for a general element of the algebra. In practice, one starts from such a generating set and the commutation relations between its elements (defining the algebra) and associates to it by a single duality function a set of dual operators with the same commutation relations up to a change of sign. In other words, one moves via the duality function from a representation of the algebra to a representation of the dual algebra.*

Remark 2.2. *The relation* (6) *is the form in which one usually formulates duality between two Markov processes. Remark however that the relation* $S_t \rightarrow^D \widehat{S}_t$ *between the semigroups is more general. It may happen that* S_t *is a Markov semigroup, whereas* $\widehat{S}_t$ *is not. E.g., mass can get lost in the evolution according to the dual semigroup* $\widehat{S}_t$*, which means* $\widehat{S}_t 1 \neq 1$*, or it can happen that* $\widehat{S}_t$ *is not a positive operator.*

In [13], the author studies the so-called duality space associated to two operators. In our notation, this is the set

$$\mathcal{D}(K, \widehat{K}) = \{D : \Omega \times \widehat{\Omega} \to \mathbb{R} : K \rightarrow^D \widehat{K}\} . \tag{7}$$

Our point of view here is to consider for a fixed duality function the set of pairs of operators $(K, \widehat{K})$ such that $K \rightarrow^D \widehat{K}$. These operators then usually form a representation and a dual representation of a given algebra, with D as inter-twiner.

In theorem 2.1 item 5, we see that we can produce new duality functions via "symmetries", i.e., operators commuting with K or $\widehat{K}$. In the context of finite sets $\Omega = \widehat{\Omega} = \{1, \ldots, n\}$, we have more: if there exists an invertible duality function D, then all other duality functions are obtained via symmetries acting on D. We formulate this more precisely in the following proposition. We will give examples in the subsequent sections.

Proposition 2.1.

1. *Let* $\Omega = \widehat{\Omega} = \{1, \ldots, n\}$*, and let* $K \rightarrow^D \widehat{K}$*. Suppose furthermore that the associated* $n \times n$ *matrix* $\mathbb{D}$ *is invertible. Then, if* $K \rightarrow^{D'} \widehat{K}$*, we have that there exists* S *commuting with* K *such that* $D' = SD$*.*

2. *For general* Ω, Ω' *we have the following. Suppose* D *and* D' *are duality functions for the duality between* K *and* $\widehat{K}$*. Suppose furthermore that* $D' = S_l D$*, for some operator* S*. Then we have*

$$(KS - SK)_l D = 0 . \tag{8}$$

In particular if D *is left exhaustive, then we conclude* $[S, K] = 0$*. Similarly, if* $D' = \widehat{S}_r D$ *then*

$$(\widehat{K}\widehat{S} - \widehat{S}\widehat{K})_r D = 0 . \tag{9}$$

and if D *is right exhaustive, then we conclude* $[\widehat{S}, \widehat{K}] = 0$ *.*

Proof. In the proof of the first item, with slight abuse of notation, we use the notation $K, \widehat{K}, D, S$ both for the operators and for their associated matrices. We have, by assumption

$$KD = D\widehat{K}^T.$$

By invertibility of D, $S = D'D^{-1}$ is well-defined and we have

$$SK = D'D^{-1}K = D'\widehat{K}^T D^{-1} \ ,$$

and

$$KS = KD'D^{-1} = D'\widehat{K}^T D^{-1} \ ,$$

hence $[K, S] = 0$.
For the second item, use $K \to^D \widehat{K}, K \to^{D'} \widehat{K}$ to conclude

$$(KS)_l D = K_l(S_l D) = K_l D' = \widehat{K}_r D' \ ,$$

as well as

$$(SK)_l D = S_l \widehat{K}_r(D) = \widehat{K}_r(S_l D) = \widehat{K}_r(D') \ ,$$

Hence

$$([S, K])_l D = 0.$$

The remaining part of the proof (for the right action case) is similar. $\square$

2.3 Self duality

Self-duality is duality between an operator and itself, i.e., referring to definition 2.2: $\Omega = \widehat{\Omega}$ and $K = \widehat{K}$. The corresponding duality function such that $K \to^D K$ is then a function $D : \Omega \times \Omega \to \mathbb{R}$ and we call it a self-duality function. For self-duality, of course, all the properties listed in theorem 2.1 hold.
In the finite case $\Omega = \{1, \dots, n\}$, a self-duality function is a $n \times n$ matrix and self-duality reads, in matrix form,

$$\mathbb{K}D = D\mathbb{K}^T \ .$$

Therefore, in this setting such a matrix D can always be found because every matrix is similar to its transposed [16], i.e., self-duality always holds with an invertible D.

Other self-duality functions can then be found by acting on a given self-duality function with symmetries of K (i.e. operators S commuting with K), as we derived in item 5 of theorem 2.1 and in proposition 2.1. In particular we have in this finite context, in the notation (7):

$$\mathcal{D}(K, K) = \{SD : [S, K] = 0\} \ , \tag{10}$$

with D an arbitrary invertible self-duality function. So this means that the correspondence between self-duality functions and symmetries of K is one-to-one. This characterization of the duality space has the advantage that the set of operators commuting with a given operator is easier to identify.

In the finite setting, if K is the generator (resp. transition operator) of a continuous-time (resp. discrete-time) Markov chain, then if this Markov chain has a reversible probability measure $\mu : \Omega \to [0,1]$, a duality function for self-duality is given by the diagonal matrix

$$D(x,y) = \delta_{x,y} \frac{1}{\mu(x)} \; .$$

This is easily verified from the detailed balance relation $\mu(x)\mathbb{K}(x,y) = \mathbb{K}(y,x)\mu(y)$. This "cheap" duality function is usually not very useful since it is diagonal, but it can be turned in a more "useful" one by acting with symmetries. All the known self-duality functions in discrete interacting particle systems such as the exclusion process, independent random walkers, the inclusion process, etc. can be obtained by this procedure [6].

3 Dualities in the context of the Heisenberg algebra.

In this section we focus on representations of Heisenberg algebra and its dual algebra, and the corresponding duality functions that connect these different representations.

3.1 Standard creation and annihilation operators

As a first example, let us start with the operators $A^\dagger, A$ working on smooth functions $f : \mathbb{R} \to \mathbb{R}$ with compact support, defined as

$$Af(x) = f'(x), \qquad A^\dagger f(x) = xf(x) \; . \tag{11}$$

These operators satisfy the canonical commutation relation $[A, A^\dagger] = I$, where I is the identity operator.
The same commutation relation, up to a negative sign, can be achieved using operators working on discrete functions. Considering

$$af(n) = nf(n-1), \qquad a^\dagger f(n) = f(n+1) \; , \tag{12}$$

acting on functions $f : \mathbb{N} \to \mathbb{R}$, we have $[a, a^\dagger] = -I$. Therefore, in view of the item 4 of theorem 2.1, the operators $a, a^\dagger$ are natural candidate for duality with $A, A^\dagger$.
To find D such that $A \to^D a$, we use the definition 2.2:

$$A_l D(x,n) = D'(x,n) = a_r D(x,n) = nD(x,n-1) \; ,$$

which yields

$$D(x,n) = \sum_{k=0}^{n} \binom{n}{k} c_{n-k} \, x^k$$

with $\{c_i : i \in \mathbb{N}\}$ a sequence of constants. In the same way, the duality condition $A^\dagger \to^D a^\dagger$, produces

$$A_l^\dagger D(x,n) = xD(x,n) = a_r^\dagger D(x,n) = D(x,n+1) ,$$

which gives

$$D(x,n) = x^n D(x,0) ,$$

with $D(x,0)$ an arbitrary function. Therefore, if we want both dualities to hold with the same duality function, then we are restricted to the choice

$$D(x,n) = c_0 x^n .$$

Without loss of generality we can choose $c_0 = 1$.

As a consequence, by using item 6 of theorem 2.1, we obtain the following result.

Theorem 3.1. *For $0 \le n \le m$, let $\alpha_n : \mathbb{R} \to \mathbb{R}$ be a finite sequence of polynomials. A differential operator of the form*

$$K = \sum_{n=0}^{m} \alpha_n(x) \frac{d^n}{dx^n} = \sum_{n=0}^{m} \alpha_n(A^\dagger) A^n$$

is dual with duality function $D(x,n) = x^n$ to

$$\widehat{K} = \sum_{n=0}^{m} a^n \alpha_n(a^\dagger) ,$$

where the operators $a, a^\dagger$ are defined in (12).

3.2 Generalization

In the following proposition we show how to generate the duality functions for more general generators $\mathbf{A}, \mathbf{A}^\dagger$ of a representation of the Heisenberg algebra, namely by repetitive action of the creation operator on the "vacuum" which is annihilated by the operator $\mathbf{A}$.

Proposition 3.1. *Suppose $[\mathbf{A}, \mathbf{A}^\dagger] = I$, and let $D(x,n)$ be functions such that*

$$\begin{aligned} (\mathbf{A}_l^\dagger)^n D(x,0) &= D(x,n) , \\ \mathbf{A}_l D(x,0) &= 0 , \end{aligned} \tag{13}$$

then $\mathbf{A} \to^D a$ and $\mathbf{A}^\dagger \to^D a^\dagger$, where $a, a^\dagger$ are the discrete representation defined in (12). *As a consequence, for a finite sequence of polynomials α_n, with $0 \le n \le m$, we have the analogue of theorem 3.1:*

$$\sum_{n=0}^{m} \alpha_n(\mathbf{A}^\dagger) \mathbf{A}^n \to^D \sum_{n=0}^{m} a^n \alpha_n(a^\dagger) .$$

Proof. We have $\mathbf{A}^\dagger \to^D a^\dagger$ by the assumption on $\mathbf{A}^\dagger$ in (13) and the definition of $a^\dagger$ in (12). We therefore have to prove $\mathbf{A} \to^D a$. Start from the commutation relation $[\mathbf{A}, \mathbf{A}^\dagger] = I$ to write

$$\mathbf{A}(\mathbf{A}^\dagger)^n = (\mathbf{A}^\dagger)^n \mathbf{A} + [\mathbf{A}, (\mathbf{A}^\dagger)^n] = (\mathbf{A}^\dagger)^n \mathbf{A} + n(\mathbf{A}^\dagger)^{n-1}.$$

Then use the assumptions (13) to deduce

$$\begin{aligned}
\mathbf{A}_l D(x,n) &= \mathbf{A}_l (a_r^\dagger)^n D(x,0) = \mathbf{A}_l (\mathbf{A}_l^\dagger)^n D(x,0) \\
&= (\mathbf{A}_l^\dagger)^n \mathbf{A}_l D(x,0) + n(\mathbf{A}_l^\dagger)^{n-1} D(x,0) = n(\mathbf{A}_l^\dagger)^{n-1} D(x,0) \\
&= n(a_r^\dagger)^{n-1} D(x,0) \\
&= nD(x,n-1) = a_r D(x,n)\ .
\end{aligned}$$

□

As an application, we can choose linear combinations of multiplication and derivative

$$\mathbf{A} = c_1 x + c_2 \frac{d}{dx}, \qquad \mathbf{A}^\dagger = c_3 x + c_4 \frac{d}{dx}, \tag{14}$$

with the real constants satisfying $c_2 c_3 - c_1 c_4 = 1$, then we satisfy the commutation relation $[\mathbf{A}, \mathbf{A}^\dagger] = I$. To find the corresponding duality function that "switches" from $\mathbf{A}, \mathbf{A}^\dagger$ to $a, a^\dagger$, we start with

$$\mathbf{A}_l D(x,0) = c_1 x D(x,0) + c_2 D'(x,0) = a_r D(x,0) = 0$$

which gives as a choice

$$D(x,0) = \exp\left(-\frac{c_1}{c_2}\frac{x^2}{2}\right)$$

and next,

$$D(x,n) = (\mathbf{A}_l^\dagger)^n D(x,0) = \left(c_3 x + c_4 \frac{d}{dx}\right)^n D(x,0).$$

An important particular case is when $c_1 = c_2 = 1/2$ and $c_3 = -c_4 = 1$. With this choice one finds that the duality function is $D(x,n) = e^{-x^2/2} H_n(x)$, where H_n is the Hermite polynomial of order n.

3.3 Dualities with two continuous variables

Within the scheme described in section 2 we can also find dualities between two operators both working on continuous variables, as the following example shows.

Consider again the operators $A, A^\dagger$ in (11). A "dual" commutation relation (in the sense of item 4 of theorem 2.1) can be obtained by considering a copy of those operators and exchanging their role. Namely, we look for dualities $d/dx \to^D y, x \to^D d/dy$. Imposing that the left action of d/dx (resp. x) does coincide with the right action of y (resp. d/dy) one finds the duality function $D(x,y) = e^{xy}$. As a consequence one immediately has the following

Theorem 3.2. *For $0 \le n \le m$, let $\alpha_n : \mathbb{R} \to \mathbb{R}$ be a finite sequence of polynomials. A differential operator working on smooth functions of the real variable x and with the generic form*

$$K = \sum_{n=0}^{m} \alpha_n(x) \frac{d^n}{dx^n}$$

is dual, with duality function $D(x,y) = e^{xy}$, to the operator working on smooth functions of the real variable y given by

$$\widehat{K} = \sum_{n=0}^{m} y^n \alpha_n(\frac{d}{dy}) \ .$$

If we specify that the operators work on functions $f : [0,\infty) \to \mathbb{R}$ and when the operators can be interpreted as generators of diffusions one has the following

Corollary 3.1. *The diffusion generator*

$$\mathscr{L} = (c_1 x^2 + c_2 x)\frac{d^2}{dx^2} + (c_3 x)\frac{d}{dx}$$

with $c_1 > 0, c_2 \ge 0$ is dual to

$$\widehat{\mathscr{L}} = c_1 y^2 \frac{d^2}{dy^2} + \left(c_2 y^2 + c_3 y\right)\frac{d}{dy}$$

with duality function $D(x,y) = e^{xy}$. For the corresponding diffusion processes $\{X_t : t \ge 0\}$, $\{Y_t : t \ge 0\}$ we thus have

$$\mathbb{E}_x e^{yX_t} = \widehat{\mathbb{E}}_y e^{xY_t} \ .$$

The particular case $c_2 = 0$ gives is that the diffusion generator $c_1 x^2 d^2/dx^2 + c_3 x d/dx$ is self-dual.

3.4 Discrete creation and annihilation operators

The following example starts from a finite dimensional representation of the Heisenberg algebra (in the spirit of [3, 9]). We consider $\Omega = \Omega_N = \{0,\ldots,N\}$ and $\widehat{\Omega} = \mathbb{N}$. For functions $f : \Omega_N \to \mathbb{R}$ we define the operators

$$\begin{aligned} \mathrm{a}_N f(k) &= (N-k)\, f(k+1) + (2k-N)\, f(k) - k f(k-1)\ , \\ \mathrm{a}_N^\dagger f(k) &= \sum_{r=0}^{k-1} (-1)^{k-1-r} \frac{\binom{N}{r}}{\binom{N}{k}} f(r)\ , \end{aligned} \tag{15}$$

with the convention $f(-1) = f(N+1) = 0$. Consider

$$D_N(k,n) = \frac{\binom{k}{n}}{\binom{N}{n}} = \frac{k(k-1)\cdots(k-(n-1))}{N(N-1)\cdots(N-(n-1))} \,. \tag{16}$$

with the convention $D_N(k,0) = 1$, $D_N(k,N+1) = 0$. Let us denote by $\mathscr{W}_N$ the vector space generated by the functions $k \mapsto D_N(k,n), 0 \le n \le N$.

Proposition 3.2.

$$\begin{aligned} (\mathrm{a}_N)_l D_N(k,n) &= nD_N(k,n-1),\ \forall\ 1 \le n, \forall\ k \ge n-1\ , \\ (\mathrm{a}_N)_l D_N(k,0) &= 0\ \forall\ 0 \le k \le N\ , \\ (\mathrm{a}^\dagger_N)_l D_N(k,n) &= D_N(k,n+1)\ \forall\ \ 0 \le n \le N, k \ge n\ . \end{aligned} \tag{17}$$

As a consequence, as operators on $\mathscr{W}_N$ we have

$$[\mathrm{a}_N, \mathrm{a}^\dagger_N] = I\ , \tag{18}$$

i.e., $\mathrm{a}_N, \mathrm{a}^\dagger_N$ form a finite dimensional representation of the canonical commutation relations.

Proof. Straightforward computation. □

Remark 3.1. *Notice that in the limit $N \to \infty$, putting $k/N = x$, and $f(k) = \phi(x) = \phi(k/N)$, $\mathrm{a}_N f(k)$ converges to $d\phi/dx$. Next, notice that $D_N(k,n) = \phi^{(n)}_N(x)$, where*

$$\phi^{(n)}_N(x) = x\left(\frac{x-\frac{1}{N}}{1-\frac{1}{N}}\right)\cdots\left(\frac{x-\frac{n-1}{N}}{1-\frac{n-1}{N}}\right)\ ,$$

converges to x^n. The effect of the operator $\mathrm{a}^\dagger_N$ on $D_N(k,n)$ is to raise the index n by one. Since $D_N(k,n) = \phi^{(n)}_N(x) \to x^n$ for $N \to \infty$ and $\mathrm{a}^\dagger_N D_N(k,n) = A^\dagger \phi^{(n)}_N(x) \to x^{n+1}$ for $N \to \infty$, we conclude that in the limit $N \to \infty$, the operator $\mathrm{a}^\dagger_N$ coincides with the multiplication operator $A^\dagger$ defined in (11).

The discrete finite dimensional representation of the Heisenberg algebra given in proposition 3.2 will be used at the end of section 4 to fit within the scheme of a change of representation the classical duality between the Moran model and the block-counting process of the Kingman coalescence. We end this section with a comment on relation between the discrete representation and Binomial distribution. This also offers an alternative simple way to see the commutation relation (18).

In many models where there is duality or self-duality, there exists a one-parameter family of invariant measures ν_ρ, and integrating the duality function w.r.t. these measures usually gives a simple expression of the parameter ρ. In the context of diffusion processes with discrete dual, this relation is usually that the duality function with n dual particles integrated over the distribution ν_ρ equals ρ^n. A similar relation connects the polynomials $D_N(k,n)$ in (16) to the binomial distribution. This general relation between a natural one-parameter family of measures and the duality functions cannot be a coincidence and requires further investigation.

The polynomials $D_N(k,n)$ are (as a function of k) indeed naturally associated to the binomial distribution. Denoting by

$$\nu_{N,\rho}(k) = \binom{N}{k}\rho^k(1-\rho)^{N-k}$$

the binomial distribution with success probability $\rho \in [0,1]$, we have

$$\sum_{k=0}^{N} D_N(k,n)\nu_{N,\rho}(k) = \rho^n \ . \tag{19}$$

For a function $f : \Omega_N \to \mathbb{R}$ we define its binomial transform $\mathscr{T}f : [0,1] \to \mathbb{R}$ by

$$(\mathscr{T}f)(\rho) = \sum_{k=0}^{N} f(k)\nu_{N,\rho}(k) \ . \tag{20}$$

If for such f, we write its expansion

$$f(k) = \sum_{r=0}^{N} c_r D_N(k,r)$$

we say that f is of degree l if $c_l \neq 0$ and all higher coefficients $c_k, k > l$ are zero. We then have, using (19) and (20),

$$(\mathscr{T}f)(\rho) = \sum_{r=0}^{N} c_r \rho^r.$$

The function f and $\mathscr{T}f$ have therefore the same components with respect to two different bases: one given by $\{D_N(k,r), r = 0,\dots,N\}$ which is a base of $\mathbb{R}^{N+1}$ and the other given by $\{\rho^r, r = 0,\dots,N\}$ which is a base of the space of polynomials on $[0,1]$ of degree at most equal to N. We then have, for all f:

$$(\mathscr{T}\mathrm{a}_N f)(\rho) = (\mathscr{T}f)'(\rho)$$

and for all f with degree less than or equal to $N-1$:

$$(\mathscr{T}\mathrm{a}_N^\dagger f)(\rho) = \rho \cdot (\mathscr{T}f)(\rho) \ .$$

This relation shows that the operators $\mathrm{a}_N, \mathrm{a}_N^\dagger$ after binomial transformation turn into the standard creation and annihilation operators $(d/d\rho, \rho)$ for a restricted set of functions (polynomials of degree at most N).

4 Classical dualities of population dynamics

The scheme developed in the section 2, together with the change of representation discussed in section 3, allows to recover many of the well-know dualities of classical models of population genetics [1, 12]. We first consider diffusion processes of the Wrigth-Fisher diffusion type and then discrete processes for a finite population of N individuals of the Moran type.

Diffusions and coalescents.
Consider smooth functions $f : [0,1] \to \mathbb{R}$ vanishing at the boundaries 0 and 1. A diffusion process on $[0,1]$ has generator of the form

$$\mathscr{L} = \alpha(x)\frac{d^2}{dx^2} + \beta(x)\frac{d}{dx} = \alpha(A^\dagger)A^2 + \beta(A^\dagger)A \;, \tag{21}$$

with A and $A^\dagger$ defined in (11). More precisely, we choose

$$\begin{aligned} \alpha(x) &= \sum_{k=1}^{\infty} \alpha_k x^k \;, \\ \beta(x) &= \sum_{k=0}^{\infty} \beta_k x^k \;, \end{aligned} \tag{22}$$

where the coefficients α_k, β_k satisfy the following

$$\begin{aligned} \alpha_2 = -\sum_{k\neq 2, k=1}^{\infty} \alpha_k, \qquad \alpha_k \geq 0 \quad \forall k \neq 2 \;, \\ \beta_1 = -\sum_{k\neq 1, k=0}^{\infty} \beta_k, \qquad \beta_k \geq 0 \quad \forall k \neq 1 \;. \end{aligned} \tag{23}$$

Typical choices are $\alpha(x) = x - x^2$, $\beta(x) = (1-x)$. By the duality $A \to^D a$, $A^\dagger \to^D a^\dagger$ and by theorem 3.1 we find that $\mathscr{L}$ is dual to

$$\begin{aligned} \hat{\mathscr{L}} f(n) &= \left(a^2\alpha(a^\dagger) + a\beta(a^\dagger)\right) f(n) \\ &= n(n-1) \sum_{k\neq 2, k=1}^{\infty} \alpha_k (f(n+k-2) - f(n)) \\ &\quad + n \sum_{k\neq 1, k=0}^{\infty} \beta_k (f(n+k-1) - f(n)) \end{aligned} \tag{24}$$

with duality function $D(x,n) = x^n$. By the conditions (23) on the coefficients, this corresponds to a Markov chain on the natural numbers.
We can then list a few examples.

1. **Wright Fisher neutral diffusion.**

$$\mathscr{L} = x(1-x)\frac{d^2}{dx^2} = A^\dagger(1-A^\dagger)A^2 \ .$$

This corresponds to $\beta = 0$ and $-\alpha_2 = \alpha_1 = 1$ and gives the dual

$$\begin{aligned} \hat{\mathscr{L}}f(n) &= \left(a^2(a^\dagger(1-a^\dagger))\right) f(n) \\ &= n(n-1)(f(n-1)-f(n)) \ , \end{aligned}$$

which is the well-known Kingman's coalescent block-counting process.

2. **Wright Fisher diffusion with mutation.**

$$\mathscr{L} = x(1-x)\frac{d^2}{dx^2} + \theta(1-x)\frac{d}{dx} = A^\dagger(1-A^\dagger)A^2 + \theta(1-A^\dagger)A \ .$$

This corresponds to $\alpha_1 = -\alpha_2 = 1$, $\beta_0 = -\beta_1 = \theta$. This gives the dual

$$\begin{aligned} \hat{\mathscr{L}}f(n) &= \left(a^2(a^\dagger(1-a^\dagger)) + \theta a(1-a^\dagger)\right) f(n) \\ &= n(n-1)(f(n-1)-f(n)) + \theta n(f(n-1)-f(n)) \ , \end{aligned}$$

which corresponds to Kingman's coalescent with extra rate θn to go down from n to $n-1$, due to mutation.

3. **Wright Fisher diffusion with "negative" selection.**

$$\mathscr{L} = x(1-x)\frac{d^2}{dx^2} - \sigma x(1-x)\frac{d}{dx} = A^\dagger(1-A^\dagger)(A^2 - \sigma A) \tag{25}$$

with $\sigma > 0$, which corresponds to $\alpha_1 = -\alpha_2 = 1$, $\beta_2 = -\beta_1 = \sigma$. The dual is

$$\begin{aligned} \hat{\mathscr{L}}f(n) &= \left((a^2 - \sigma a)a^\dagger(1-a^\dagger)\right) f(n) \\ &= n(n-1)(f(n-1)-f(n)) + \sigma n(f(n+1)-f(n)) \end{aligned}$$

4. **Stepping stone model.** This is an extension of the Wright-Fisher diffusion, modelling subpopulations of which the individuals have two types, and which evolve within each subpopulation as in the neutral Wright Fisher diffusion, and additionally, after reproduction a fraction of each subpopulation is exchanged with other subpopulations. These subpopulations are indexed by a countable set S. The variables $x_i \in [0,1], i \in S$ then represent the fraction of type 1 in the i^{th} subpopulation. The generator of this model is defined on smooth functions on the set $\Omega = [0,1]^S$ and given by

$$\mathscr{L} = \sum_{i,j\in S} p(i,j)(x_j - x_i)\left(\frac{\partial}{\partial x_i} - \frac{\partial}{\partial x_j}\right) + \sum_{i\in S} x_i(1-x_i)\frac{\partial^2}{\partial x_i^2} \ . \tag{26}$$

Here $p(i,j)$, with positive entries outside of the diagonal and with $\sum_{j\in S} p(i,j) = 1$, is an irreducible random walk kernel on the set S.

In terms of the standard creation and annihilation operators $A_i^\dagger = x_i, A_i = \frac{\partial}{\partial x_i}$, this generator reads

$$\mathscr{L} = \sum_{i,j\in S} p(i,j)(A_j^\dagger - A_i^\dagger)(A_i - A_j) + \sum_{i\in S} A_i^\dagger(1-A_i^\dagger)A_i^2 \qquad (27)$$

The dual operators act on $f: \mathbb{N}^S \to \mathbb{R}$ via $a_i f(n) = n_i f(n-e_i), a_i^\dagger f(n) = f(n+e_i)$, where $n \in \mathbb{N}^S$ and $e_i \in \mathbb{N}^S$ is the i-th canonical unit vector defined via $(e_i)_j = \delta_{i,j}$. By theorem 2.1 item 7, we have $A_i \to^D a_i, A_i^\dagger \to^D a_i^\dagger$ with

$$D(n,x) = \prod_{i\in S} x_i^{n_i} \;.$$

As a consequence the generator $\mathscr{L}$ in (27) is dual to $\hat{\mathscr{L}}$ given by

$$\hat{\mathscr{L}} = \sum_{i,j\in S} p(i,j)(a_i - a_j)(a_j^\dagger - a_i^\dagger) + \sum_{i\in S} a_i^2 a_i^\dagger(1-a_i^\dagger) \qquad (28)$$

or equivalently the generator $\mathscr{L}$ in (26) is dual to $\hat{\mathscr{L}}$ given by

$$\begin{aligned}\hat{\mathscr{L}}f(n) \;&=\; \sum_{i,j\in S} p(i,j)n_i(f(n-e_i+e_j)-f(n))\\ &+\; \sum_{i,j\in S} p(j,i)n_j(f(n+e_i-e_j)-f(n))\\ &+\; \sum_{i\in S} n_i(n_i-1)(f(n_i-e_i)-f(n)) \;, \qquad (29)\end{aligned}$$

which is the generator of a Markov process on $\mathbb{N}^S$ with transitions $n \to n-e_i+e_j$ (resp. $n \to n-e_j+e_i$) at rate $n_i p(i,j)$ (resp. $n_j p(j,i)$) and $n \to n-e_i$ at rate $n_i(n_i-1)$. The first type of transitions are of random walk type and correspond to the exchange of subpopulations, whereas the second type are the transitions corresponding to the Kingmans' coalescent in each subpopulation.

Finite-size populations [2, 5] and coalescents.
As a final example, we illustrate the use of the discrete creation and annihilation operators $a_N^\dagger, a_N$, corresponding to population models with N individuals in the discrete Moran model. This is the discrete analogue of the neutral Wright-Fisher diffusion

$$\mathscr{L}_N f(k) = \frac{N^2}{2}\frac{k}{N}\left(1-\frac{k}{N}\right)(f(k+1)+f(k-1)-2f(k)) \;. \qquad (30)$$

In terms of the discrete creation and annihilation operators $\mathrm{a}_N, \mathrm{a}_N^\dagger$ defined in (15), this generator reads

$$\mathscr{L}_N = \mathrm{a}_N^\dagger (1 - \mathrm{a}_N^\dagger) \mathrm{a}_N^2 \ . \tag{31}$$

By theorem 2.1 and proposition 3.2, we therefore obtain immediately that this generator is dual to the generator of the Kingman's coalescent with duality function (16).

5 $SU(1,1)$ algebra and corresponding dualities

In this section we show new dualities for models of population dynamics, using dualities between well-chosen differential operators and discrete operators. These operators have been used in the context of particle systems and models of heat conduction [6]. Interpreted here in terms of population models, they yield in that context new dualities.

We start with the following two families (labeled by m) of infinite dimensional representations of the algebra $SU(1,1)$. The first family of operators act on functions $f : [0, \infty) \to \mathbb{R}$, whereas the second family acts on functions $f : \mathbb{N} \to \mathbb{R}$.

$$\begin{aligned} \mathscr{K}^+ &= z \ , \\ \mathscr{K}^- &= z \frac{d^2}{dz^2} + \frac{m}{2} \frac{d}{dz} \ , \\ \mathscr{K}^0 &= z \frac{d}{dz} + \frac{m}{4} \ , \end{aligned} \tag{32}$$

and

$$\begin{aligned} K^+ f(n) &= \left(\frac{m}{2} + n \right) f(n+1) \ , \\ K^- f(n) &= n f(n-1) \ , \\ K^0 f(n) &= \left(\frac{m}{4} + n \right) f(n) \ . \end{aligned} \tag{33}$$

The $\mathscr{K}$ operators satisfy the $SU(1,1)$ commutation relations

$$[\mathscr{K}^o, \mathscr{K}^\pm] = \pm \mathscr{K}^\pm \ , \qquad\qquad [\mathscr{K}^-, \mathscr{K}^+] = 2\mathscr{K}^o \ , \tag{34}$$

whereas the K operators satisfy the dual commutation relations (i.e., with opposite sign). Therefore, the operators are candidates for a duality relation. To find the duality function $d : [0, \infty) \times \mathbb{N} \to \mathbb{R}$ we use

$$\mathscr{K}_l^- d(z,0) = \left(z \frac{d^2}{dz^2} + \frac{m}{2} \frac{d}{dz} \right) d(z,0) = K_r^- d(z,0) = 0$$

which gives as a possible choice $d(z,0) = 1$. Then, we can act with $\mathscr{K}^+$:

$$(\mathscr{K}_l^+)^n d(z,0) = z^n = (K_r^+)^n d(z,0) = \frac{m}{2} \left(\frac{m}{2} + 1 \right) \ldots \left(\frac{m}{2} + n - 1 \right) d(z,n) \ ,$$

and we find

$$d(z,n) = \frac{z^n}{\frac{m}{2}\left(\frac{m}{2}+1\right)\dots\left(\frac{m}{2}+n-1\right)} = \frac{z^n\Gamma\left(\frac{m}{2}\right)}{\Gamma\left(\frac{m}{2}+n\right)}\,. \tag{35}$$

One then easily verifies that also $\mathscr{K}_l^- d(z,n) = K_r^- d(z,n)$ and $\mathscr{K}_l^0 d(z,n) = K_r^0 d(z,n)$. We can summarize our findings in the following proposition.

Proposition 5.1. *The family of operators given by* (32) *and the family of operators given by* (33) *are dual with duality function given by* (35). *As a consequence, every element of the algebra generated by the operators* (32) *is dual to an element of the algebra generated by* (33), *obtained by replacing the operators by their duals and reverting the order of products.*

5.1 Generators from $SU(1,1)$ raising and lowering operators

The relevance of the $K^{\pm}, \mathscr{K}^{\pm}$ lies in the fact that some natural generators of diffusion processes of population dynamics can be rewritten in terms of them. We start now with defining these generators.

Definition 5.1 ([4], p. 55)**.** *The d-types Wright-Fisher model with symmetric parent-independent mutation at rate $\theta \in \mathbb{R}$ is a diffusion process on the simplex $\sum_{i=1}^d x_i = 1$ defined by the generator*

$$\begin{aligned}\mathscr{L}_{d,\theta}^{WF} g(x) &= \sum_{i=1}^{d-1} \frac{1}{2} x_i(1-x_i)\frac{\partial^2 g(x)}{\partial x_i^2} - \sum_{1\le i<j\le d-1} x_i x_j \frac{\partial^2 g(x)}{\partial x_i \partial x_j} \\ &+ \frac{\theta}{d-1}\sum_{i=1}^{d-1}(1-dx_i)\frac{\partial g(x)}{\partial x_i}\,. \end{aligned}\tag{36}$$

Definition 5.2. *The Brownian Energy process with parameter $m \in \mathbb{R}$ on the complete graph with d vertices (BEP(m)) is a diffusion on $\mathbb{R}_+^d$ with generator*

$$\begin{aligned}\mathscr{L}_d^{BEP(m)} f(y) &= \frac{1}{2}\sum_{1\le i<j\le d} y_i y_j \left(\frac{\partial}{\partial y_i} - \frac{\partial}{\partial y_j}\right)^2 f(y) \\ &- \frac{m}{4}\sum_{1\le i<jd}(y_i - y_j)\left(\frac{\partial}{\partial y_i} - \frac{\partial}{\partial y_j}\right) f(y)\,. \end{aligned}\tag{37}$$

Proposition 5.2. *The Brownian Energy process with parameter $m \in \mathbb{R}$ on the complete graph with d vertices and with initial condition $\sum_{i=1}^d x_i = 1$ coincides with the d-types Wright-Fisher model with symmetric parent-independent mutation at rate $\theta = \frac{m}{4}(d-1)$.*

Proof. The statement of the proposition is a consequence of the fact the BEP evolution conserves the quantity $x_1 + \ldots + x_d$. Consider the initial condition $\sum_{i=1}^{d} x_i = 1$ and define the function $\phi : \mathbb{R}^{d-1} \to \mathbb{R}^d$ such that

$$(x_1, \ldots, x_{d-1}) = x \mapsto \phi(x) = (x_1, \ldots, x_{d-1}, 1 - \sum_{j=1}^{d-1} x_j) .$$

Then $g(x) = f(\phi(x))$ and, for all $i = 1, \ldots, d-1$, using the chain rule gives

$$\frac{\partial g(x)}{\partial x_i} = \frac{\partial f(\phi(x))}{\partial y_i} - \frac{\partial f(\phi(x))}{\partial y_d} .$$

A computation shows that

$$\mathscr{L}_d^{BEP(m)} f(x_1, \ldots, x_{d-1}, x_d) = \mathscr{L}_{d,\frac{m}{4}(d-1)}^{WF} g(x_1, \ldots, x_{d-1}) .$$

□

Definition 5.3. *The d-types Moran model with population size N and with symmetric parent-independent mutation at rate θ has generator*

$$\begin{aligned} &\mathscr{L}_{N,d,\theta}^{Mor} g(k) = \\ &\frac{1}{2} \sum_{1 \le i < j \le d-1} k_i \left(k_j + \frac{2\theta}{d-1} \right) (g(k + e_i - e_j) + g(k - e_i + e_j) - 2g(k)) \\ &+ \frac{1}{2} \sum_{i=1}^{d-1} k_i \left(N - \sum_{j=1}^{d-1} k_j + \frac{2\theta}{d-1} \right) (g(k + e_i) + g(k - e_i) - 2g(k)) . \end{aligned} \tag{38}$$

Definition 5.4. *The Symmetric Inclusion process with parameter $m \in \mathbb{R}$ on the complete graph with d vertices (SIP(m)) is a Markov process on $\mathbb{N}_+^d$ with generator*

$$\begin{aligned} &\mathscr{L}_d^{SIP(m)} f(k) = \\ &\frac{1}{2} \sum_{1 \le i < j \le d} k_i \left(k_j + \frac{m}{2} \right) (f(k + e_i - e_j) + f(k - e_i + e_j) - 2f(k)) . \end{aligned} \tag{39}$$

Proposition 5.3. *The generator of the Symmetric Inclusion process with parameter $m \in \mathbb{R}$ on the complete graph with d vertices and with initial condition $\sum_{i=1}^{d} n_i = N$ coincides with the generator of the d-types Moran model with population size N and with symmetric parent-independent mutation at rate $\theta = \frac{m}{4}(d-1)$.*

Proof. One verifies that

$$\mathscr{L}_d^{SIP(m)} f(k_1,\dots,k_{d-1},k_d) = \mathscr{L}^{Mor}_{N,d,\frac{m}{4}(d-1)}\, g(k_1,\dots,k_{d-1})$$

with

$$g(k_1,\dots,k_{d-1}) = f(k_1,\dots,k_{d-1},N-\sum_{j=1}^{d-1}k_j)\ .$$

□

We can now state our duality result.

Theorem 5.1. *In the presence of symmetric parent-independent mutation at rate θ, the d-types Wright-Fisher diffusion process with generator (36) and the d-types Moran model with N individuals and with generator (38) are dual with duality function*

$$\tilde{D}_N(x,k) = \prod_{i=1}^{d} \frac{x_i^{k_i}}{\Gamma(\frac{2\theta}{d-1}+k_i)}\ , \tag{40}$$

with

$$x_d = 1-\sum_{j=1}^{d-1}x_j\ , \qquad\qquad k_d = N-\sum_{j=1}^{d-1}k_j\ .$$

Proof. The statement of the theorem is a consequence of the duality between BEP(m) and SIP(m), which we now recall. We consider the two families of operators representing the $SU(1,1)$ and dual $SU(1,1)$ commutation relations, now rewritten in d coordinates:

$$\begin{cases} \mathscr{K}^+_{m,i} = x_i \\ \\ \mathscr{K}^-_{m,i} = x_i\,\frac{\partial^2}{\partial {x_i}^2}+\frac{m}{2}\frac{\partial}{\partial x_i} \\ \\ \mathscr{K}^0_{m,i} = x_i\,\frac{\partial}{\partial x_i}+\frac{m}{4} \end{cases} \tag{41}$$

and the corresponding discrete operators

$$\begin{cases} \mathrm{K}^+_{m,i} f(k_i) = \left(k_i+\frac{m}{2}-1\right) f(k_i-1) \\ \\ \mathrm{K}^-_{m,i} f(k_i) = (k_i+1) f(k_i+1) \\ \\ \mathrm{K}^o_{m,i} f(k_i) = \left(k_i+\frac{m}{4}\right) f(k_i)\ . \end{cases} \tag{42}$$

The generator of the BEP(m) then reads

$$\mathscr{L}_m = \frac{1}{2}\sum_{1\le i<j\le d}\left(\mathscr{K}^+_{m,i}\mathscr{K}^-_{m,j}+\mathscr{K}^-_{m,i}\mathscr{K}^+_{m,j}-2\mathscr{K}^o_{m,i}\mathscr{K}^o_{m,j}+\frac{m^2}{8}\right)\ , \tag{43}$$

By proposition 5.1, combined with theorem 2.1, we find that this operator is dual to the operator

$$\mathrm{L}_m = \frac{1}{2} \sum_{1\le i<j\le d} \left(\mathrm{K}^+_{m,i}\mathrm{K}^-_{m,j} + \mathrm{K}^-_{m,i}\mathrm{K}^+_{m,j} - 2\mathrm{K}^o_{m,i}\mathrm{K}^o_{m,j} + \frac{m^2}{8} \right) , \tag{44}$$

This operator is exactly the generator of the SIP(m). The duality function is given by, using once more theorem 2.1, item 7:

$$D_N(x,k) = \prod_{i=1}^{d} d(x_i,k_i) \ .$$

where $d(z,k)$ is given in (35). The multiplicative constant $\Gamma(m/2)$ in (35) can be dropped, and the result of the theorem thus follows from combining the duality between BEP(m) and SIP(m) with proposition 5.2 and proposition 5.3. □

5.2 Duality between d-types Wright-Fisher diffusion and d-types Moran model

We can now also let $m \to 0$, or correspondingly $\theta \to 0$ to obtain a duality result between the neutral Wright-Fisher diffusion and the standard Moran model.

Let $d \ge 2$ be an integer denoting the number of types (or alleles) in a population.

Definition 5.5. *The d-types Wright-Fisher model is a diffusion process on the simplex $\sum_{i=1}^d x_i = 1$ defined by the generator*

$$\mathscr{L}_d^{WF} g(x) = \sum_{i=1}^{d-1} \frac{1}{2} x_i(1-x_i) \frac{\partial^2 g(x)}{\partial x_i^2} - \sum_{1\le i<j\le d-1} x_i x_j \frac{\partial^2 g(x)}{\partial x_i \partial x_j} \ . \tag{45}$$

Definition 5.6. *The Brownian Energy process with $m = 0$ on the complete graph with d vertices is a diffusion on $\mathbb{R}^d_+$ given by the generator*

$$\mathscr{L}_d^{BEP(0)} f(y) = \frac{1}{2} \sum_{1\le i<j\le d} y_i y_j \left(\frac{\partial}{\partial y_i} - \frac{\partial}{\partial y_j} \right)^2 f(y) \ . \tag{46}$$

Proposition 5.4. *The generator of the Brownian Energy process with $m = 0$ on the complete graph with d vertices and with initial condition $\sum_{i=1}^d x_i = 1$ does coincide with the generator of the d-types Wright-Fisher diffusion, i.e.*

$$\mathscr{L}_d^{BEP(0)} f(x_1,\ldots,x_{d-1},x_d) = \mathscr{L}_d^{WF} g(x_1,\ldots,x_{d-1})$$

with

$$g(x_1,\ldots,x_{d-1}) = f(x_1,\ldots,x_{d-1},1-\sum_{j=1}^{d-1}x_j)\ .$$

Proof. Similar to the proof of proposition 5.2 $\square$

Definition 5.7. *In the d-types Moran model with population size N a pair of individuals of types i and j are sampled uniformly at random, one dies with probability $1/2$ and the other reproduces. Therefore, denoting by $k=(k_1,\ldots,k_{d-1})$, where k_i is the number of individuals of type i, the process has generator*

$$\begin{aligned}\mathscr{L}_{N,d}^{Mor} g(k) &= \frac{1}{2}\sum_{1\le i<j\le d-1} k_i k_j\ (g(k+e_i-e_j)+g(k-e_i+e_j)-2g(k)) \\ &+ \frac{1}{2}\sum_{i=1}^{d-1} k_i\left(N-\sum_{j=1}^{d-1}k_j\right)(g(k+e_i)+g(k-e_i)-2g(k))\ .\end{aligned} \tag{47}$$

Definition 5.8. *The Symmetric Inclusion process with $m=0$ on the complete graph with d vertices is a Markov process on $\mathbb{N}_+^d$ with generator*

$$\mathscr{L}_d^{SIP(0)} f(k) = \frac{1}{2}\sum_{1\le i<j\le d} k_i k_j (f(k+e_i-e_j)+f(k-e_i+e_j)-2f(k))\ . \tag{48}$$

Proposition 5.5. *The generator of the Symmetric Inclusion process with $m=0$ on the complete graph with d vertices and with initial condition $\sum_{i=1}^d n_i = N$ does coincide with the generator of the d-types Moran model with population size N, i.e.*

$$\mathscr{L}_d^{SIP(0)} f(k_1,\ldots,k_{d-1},k_d) = \mathscr{L}_{N,d}^{Mor} g(k_1,\ldots,k_{d-1})$$

with

$$g(k_1,\ldots,k_{d-1}) = f(k_1,\ldots,k_{d-1},N-\sum_{j=1}^{d-1}k_j)\ .$$

Proof. Similarly to the proof of proposition 5.3, the result follows from the conservation law, namely the fact that the SIP evolution conserves the total number of particles $k_1+\ldots+k_d$. $\square$

In the duality result of theorem 5.1 we cannot directly substitute $m=0$ because there would be problems when some $k_i=0$. To state a duality

result for $\theta = 0$, i.e., between the Wright Fisher diffusion and the Moran model without mutation, we start again from the duality between Brownian Energy process and Symmetric Inclusion process:

$$\mathbb{E}_x^{BEP(m)}\left(\prod_{i=1,\xi_i\geq 1}^{d} \frac{x_i(t)^{\xi_i}}{\frac{m}{2}\dots\left(\frac{m}{2}+\xi_i-1\right)}\right) \tag{49}$$

$$= \mathbb{E}_\xi^{SIP(m)}\left(\prod_{i=1,\xi_i(t)\geq 1}^{d} \frac{x_i^{\xi_i(t)}}{\frac{m}{2}\dots\left(\frac{m}{2}+\xi_i(t)-1\right)}\right).$$

For $\xi \in \mathbb{N}^d$, denote $\mathscr{R}(\xi) = \{i : \xi_i \geq 1\}$. Then we can rewrite (49) and obtain

$$\mathbb{E}_x^{BEP(m)}\left(\prod_{i=1,\xi_i\geq 1}^{d} \frac{x_i(t)^{\xi_i}}{\left(\frac{m}{2}+1\right)\dots\left(\frac{m}{2}+\xi_i-1\right)}\right) \tag{50}$$

$$= \mathbb{E}_\xi^{SIP(m)}\left(\prod_{i=1,\xi_i(t)\geq 1}^{d} m^{\mathscr{R}(\xi)-\mathscr{R}(\xi_t)} \frac{x_i^{\xi_i(t)}}{\left(\frac{m}{2}+1\right)\dots\left(\frac{m}{2}+\xi_i(t)-1\right)}\right).$$

Notice that in the $SIP(0)$ process, only coalescence jumps take place, hence $\mathscr{R}(\xi(t)) \leq \mathscr{R}(\xi)$ for all $t > 0$, $\xi \in \mathbb{N}^d$. Now we are in the position to take the limit $m \to 0$ and we find

$$\mathbb{E}_x^{BEP(0)}\left(\prod_{i=1,\xi_i\geq 1}^{d} \frac{x_i(t)^{\xi_i}}{(\xi_i-1)!}\right) \tag{51}$$

$$= \mathbb{E}_\xi^{SIP(0)}\left(I\left(\mathscr{R}(\xi)=\mathscr{R}(\xi(t))\right)\prod_{i:\xi_i(t)\geq 1} \frac{x_i{}^{\xi_i(t)}}{(\xi_i(t)-1)!}\right).$$

Notice that the lhs becomes zero as soon as one of the x_i are zero, which corresponds to the fact that for all i, $x_i = 0$ is an absorbing set in the diffusion. Corresponding to this, the rhs becomes zero as soon as one of the species disappear, i.e., as soon as $\mathscr{R}(\xi)$ decreases by one unit. We call (51) "*duality until absorption with duality function*"

$$D(\xi, x) = \left(\prod_{i=1,\xi_i\geq 1}^{d} \frac{x_i^{\xi_i}}{(\xi_i-1)!}\right). \tag{52}$$

We can summarize our findings in the following theorem.

Theorem 5.2. *The d-types Wright-Fisher diffusion process with generator (45) and the d-types Moran model with N individuals and with generator*

(47) are dual until absorption on duality function

$$\tilde{D}_N(x,k) = \prod_{i=1}^{d} \frac{x_i^{k_i}}{(k_i-1)!} \ , \tag{53}$$

with

$$x_d = 1 - \sum_{j=1}^{d-1} x_j \ , \qquad k_d = N - \sum_{j=1}^{d-1} k_j \ .$$

Remark 5.1. *We remark that the duality results in subsections 5.1 and 5.2 are of a different nature than the usual dualities between forward process and coalescent. Indeed, we have here duality between two "forward processes" (the Wright-Fisher diffusion and the Moran model), which cannot be obtained from "looking backwards in time", the method by which moment-dualities with the coalescent are usually obtained. In our framework, the dualities with the coalescent correspond to a change of representation in the Heisenberg algebra, whereas the dualities between e.g. Wright-Fisher and Moran model arise from a change of representation in the $SU(1,1)$ algebra.*

5.3 Self-duality of the d-types Moran model

We can push further the $SU(1,1)$ structure behind the Moran model and deduce self-duality of the process.

Theorem 5.3. *The d-types Moran model with N individuals and with generator (38) is self-dual with duality function*

$$\bar{D}_N(k,\xi) = \prod_{i=1}^{d} \frac{k_i!}{(k_i-\xi_i)!} \frac{\Gamma\left(\frac{2\theta}{d-1}\right)}{\Gamma\left(\xi_i + \frac{2\theta}{d-1}\right)} \ , \tag{54}$$

where $k_d = N - \sum_{i=1}^{d-1} k_i$ and $\xi_d = N - \sum_{i=1}^{d-1} \xi_i$.

Proof. The result follows from the self-duality property of the SIP(m) process [8] and from proposition 5.3. $\square$

The limit $m \to 0$, or equivalently $\theta \to 0$, leads to the self-duality until absorption relation

$$\begin{aligned} & \mathbb{E}_\eta^{SIP(0)}\left(\prod_{i=1,\xi_i\geq 1}^{d} \frac{\eta_i(t)!}{(\eta_i(t)-\xi_i)!(\xi_i-1)!}\right) \qquad (55)\\ = \ & \mathbb{E}_\eta^{SIP(0)}\left(I(\mathscr{R}(\xi(t))=\mathscr{R}(\xi)) \prod_{i=1,\xi_i(t)\geq 1}^{d} \frac{\eta_i!}{(\eta_i-\xi_i(t))!(\xi_i(t)-1)!}\right) \ . \end{aligned}$$

This computation then leads to the following theorem.

Theorem 5.4. *The d-types Moran model with N individuals and with generator (47) is self-dual until absorption, with duality function*

$$\bar{D}_N(k,\xi) = \prod_{i=1,\xi_i\geq 1}^{d} \left(\frac{k_i}{(\xi_i-1)!}\right) , \tag{56}$$

where $k_d = N - \sum_{i=1}^{d-1} k_i$ and $\xi_d = N - \sum_{i=1}^{d-1} \xi_i$.

5.4 Examples

We give some examples of concrete computations using the dualities of the present section.

1. Heterozygosity of two-types Wright-Fisher diffusion. This is exactly the $BEP(0)$, x_t, y_t on two sites, with initial condition $x, y : x + y = 1$.

$$\begin{aligned} \mathbb{E}_{x,y}^{BEP(0)}(x(t)y(t)) &= \mathbb{E}_{1,1}^{SIP(0)}(xyI(n_1(t)=1, n_2(t)=1)) \\ &= xy\mathbb{P}_{1,1}(n_1(t)=1, n_2(t)=1) = xye^{-t} , \end{aligned}$$

   where $\mathbb{P}_{1,1}$ denotes the law of the $SIP(0)$ process initialized with one particle per site.

2. Higher moments of two-types Wright-Fisher diffusion. We use the same notation of the previous item and consider for instance x^2y. Further, we notice that if we start the $SIP(0)$ from initial configuration $(n_1, n_2) = (2,1)$, then the only transitions before absorption are of the type $(2,1) \to (1,2)$ and vice versa, and both transitions occur at rate 2, whereas from any of these states, the rate to go to the absorbing states is also equal to two. Therefore,

$$\begin{aligned} &\mathbb{E}_{xy}^{BEP(0)}(x^2(t)y(t)) \\ &= x^2y\mathbb{P}_{2,1}^{SIP(0)}((n_1(t),n_2(t)) = (2,1)) + xy^2\mathbb{P}_{2,1}^{SIP(0)}((n_1(t),n_2(t)) = (1,2)) \\ &= \frac{e^{-2t}}{2}(x^2y(1+e^{-2t}) + xy^2(1-e^{-2t})) . \end{aligned}$$

3. Analogue of heterozygosity for d-types Wright Fisher diffusion. Notice that for multitype Wright Fisher, there is no simple analogue of the Kingman's coalescent, as for the two-types case. This means that we have the $BEP(0)$ started from $x_1, \ldots, x_d$

$$\begin{aligned} &\mathbb{E}_{x_1,\ldots,x_d}^{BEP(0)}(x_1(t)\ldots x_d(t)) \\ &= x_1\ldots x_d\mathbb{E}_{(1,1,\ldots,1)}^{SIP(0)}(I(n_i(t)\neq 0 \ \ \forall i \in \{1,\ldots,d\})) \\ &= x_1\ldots x_d e^{-(d-1)t} . \end{aligned}$$

4. Analogue of x^2y for the multi-type case.

$$\begin{aligned}
&\mathbb{E}^{BEP(0)}_{x_1,\dots,x_d}(x_1^2(t)x_2\dots x_d(t)) \\
&= x_1\dots x_d\mathbb{E}^{SIP(0)}_{(2,1,\dots,1)}\left(I(n_i(t)\neq 0 \ \ \forall i\in\{1,\dots,d\})\right) \\
&= \sum_{i=1}^{d}\left(\prod_{j\neq i} x_j\right) x_i^2\mathbb{P}^{SIP(0)}_{(2,1,\dots,1)}(n_1(t)=1,\dots,n_i(t)=2,\dots,n_d(t)=1)\ .
\end{aligned}$$

To compute the latter probability, we remark that starting from the configuration $(2,1,\dots,1)$, the $SIP(0)$ will be absorbed as soon as one of the particles on the sites with a single occupation makes a jump, which happens at rate $(d-1)(d-2)+(d-1)2 = d(d-1)$. Further, as long as absorption did not occur, the site with two particles moves as a continuous-time random walk X_t^d on the complete graph of d vertices, moving at rate 2 and starting at site 1. Therefore

$$\begin{aligned}
&\mathbb{P}^{SIP(0)}_{(2,1,\dots,1)}(n_1(t)=1,\dots,n_i(t)=2,\dots,n_d(t)=1) \\
&= e^{-d(d-1)t}\mathbb{P}(X_t^d = i) \\
&= e^{-2dt}+\frac{1}{d}(1-e^{-2dt})\delta_{i,1}+(1-\delta_{i,1})\frac{1}{d}(1-e^{-2dt})\ .
\end{aligned}$$

As these examples illustrate, computations of moments in the multi-type Wright Fisher model reduce to finite dimensional Markov chain computations, associated to inclusion walkers on the complete graph until absorption, which occurs as soon as a site becomes empty. The same can be done for the multi-type Moran model, using its self-duality.

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